

EVIDENCE FOR THE HYBRID ORIGIN OF PETASITES WARRENI AND P. VITIFOLIUS

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The purpose of this paper is to present evidence for the hybrid origin of *Petasites warrenii* St. John, an endemic to the State of Washington. This interpretation is based on the study of herbarium specimens, on observations in the field of reproductive biology and distribution, and on the progeny from artificial hybridizations involving *P. warrenii* and its putative parents, *P. frigidus* var. *palmatus* (Ait.) Cronq. and *P. sagittatus* (Pursh) Gray. A portion of the evidence also suggests that *P. vitifolius* Greene, which has a much wider distribution across North America, is a product of the same hybridization complex which has produced *P. warrenii*.

TAXONOMIC HISTORY

The circumboreal genus *Petasites* Mill. (Compositae-Senecioneae) is represented in North America by four ill-defined native taxa, and two introduced species which have escaped from cultivation (*P. japonicus* Maxim., and *P. hybridus* (L.) Gaertn., Mey. & Sherb.). The systematics of the indigenous members is based almost entirely on leaf shape, and was last revised by Cronquist (1946, 1953). As a result of his revision the numerous species described from this continent up to that time (cf. Rydberg 1927) were reduced to only two, *P. sagittatus* (Pursh) Gray (Fig. 1B), and the polymorphic *P. frigidus* (L.) Fries, with three varieties: var. *frigidus* (Fig. 1K, L), var. *nivalis* (Greene) Cronq. (Fig. 1H, J), and var. *palmatus* (Ait.) Cronq. (Fig. 1A). The following key to the species and varieties is taken from those of Cronquist (1953, varieties of *P. frigidus*; 1955, *P. sagittatus*.)

1. Leaves evidently lobed, varying to coarsely few-toothed with 5-15 teeth on each side. *P. frigidus*

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2. Leaves merely coarsely toothed or very shallowly and obscurely lobed: circumboreal, characteristically arctic, extending south, uncommonly, to central Washington. var. *frigidus*
2. Leaves evidently lobed.
 3. Leaves palmately or more often pinnipalmately lobed and veined, the lobes ordinarily not extending more than halfway to the base (or often deeper in western specimens, which are distinctly pinnipalmate); leaves seldom more than 2 dm. wide, seldom evidently wider than long; characteristically subarctic or of boreal forests, extending south to the Gaspé Peninsula of Quebec, northern Minnesota, and at high elevations in the mountains to northern Quebec. var. *nivalis*
 3. Leaves palmately lobed and veined, the lobes commonly extending well over half way to the base (or in western specimens often only about half way to the base); leaves tending to be broader than long, often very large (up to 4 dm. wide); more southern than the other varieties, extending south to California, Minnesota, Michigan, and Massachusetts. var. *palmatus*
1. Leaves varying from merely a little wavy and callous-denticulate to more commonly conspicuously dentate with 20 to 45 teeth on each side. Wet places; Alaska to Labrador, south to northeastern Washington, northern Idaho, Montana to Colorado, northern Minnesota and Wisconsin. *P. sagittatus*

This system was not without precedent. Hooker (1833) first suggested that the North American taxa might best be considered as varieties of a single species. Under the generic name of *Nardosmia* Cass. he recognized four distinct species (*N. frigida* Hook., *N. corymbosa* Hook., *N. palmata* Hook., and *N. sagittata* Hook.), but noted that they "are distinguished by very slight characters, and the numerous specimens before me, would, in the varied form of the foliage, lead to the suspicion that they in reality constitute but one species."

Herder (1865) reduced *Nardosmia palmata* and *N. corymbosa* to varietal status under *N. frigida*, but his revision went unheeded by North American taxonomists, who subsequently described several minor morphological variants as distinct species.

Rydberg (1927, pp. 310-315) recognized eleven distinct species, and in the fifteen years following his publication at least two new species and one variety were described.

It was to Herder's system that Cronquist especially referred in again revising the taxonomy of the group. The interested reader may consult his papers (1946, 1953, 1955) for comments and synonymy. This classification is now found in several major floristic works published within the past dozen years, and its nomenclature is followed here. It has been rejected by Hultén (1950, p. 1583), however, and is not followed by such authors as Anderson (1959), Moss (1960), and Polunin (1959).

Cronquist (1946) tentatively placed *Petasites warrenii* (Fig. 1D) in synonymy under var. *frigidus*, and later (1955) stated that in leaf form it was "approaching var. *nivalis*. Perhaps eventually to be recognized as a distinct variety." He also (1946) reduced *P. vitifolius* Greene (Fig. 1E, G; incl. *P. trigonophyllus* Greene) to synonymy under var. *nivalis*.

The peculiarities of form and distribution of *Petasites warrenii* prompted this investigation of the taxon, and of the possibility of interspecific relationships between *P. frigidus* var. *palmatus* and *P. sagittatus*.

MATERIALS AND METHODS

In the course of this study more than 1000 herbarium specimens of the North American taxa were examined. Those specimens which are considered to have originated in the complex of hybridization described here are listed below under a separate heading.

In the field the limits of distribution of *Petasites warrenii* were ascertained, and observations made on the nature of its inflorescences and reproduction. Live female plants of *P. warrenii* and *P. sagittatus* were transferred from the field to cultivation in the greenhouse for later use in artificial pollinations.

Artificial pollinations were made both in the field and in the greenhouse in the spring of 1960. In the greenhouse pollen from male plants of *Petasites frigidus* var. *palmatus* growing on the road embankment of U. S. 10, about one mile east of Issaquah, Washington, was transferred to flowers of female plants of both *P. sagittatus*, collected near Bona-

parte Lake, Okanogan Co., Washington, and *P. warrenii*, collected near Liberty, Kittitas Co., Washington. Pollinations were made and plants kept in insect-proof cages.

In the field, female flowers of *Petasites warrenii*, blooming near Liberty, were pollinated by flowers of male inflorescences of *P. frigidus* var. *palmatus* blooming near the summit of Snoqualmie Pass, Washington (a linear distance from Liberty of approximately forty miles). The pollinated inflorescences were protected from insects by covering the scapes with a nylon stocking, the lower, open end of which was tied shut around the scape and supporting wire frame.

Pollen was applied to the protruding styles of as many flowers and heads as possible. It could not be determined which styles were in a receptive condition, or how many received pollen. In both locations adjacent flowering inflorescences were left unpollinated as a simple test for natural pollination. Unfortunately, male plants of *Petasites sagittatus* were not available for making reciprocal crosses, and male plants of *P. warrenii* are unknown.

OBSERVATIONS AND RESULTS

Reproductive biology

All of the North American *Petasites* are polygamodioecious, rhizomatous, herbaceous perennials, utilizing both sexual and asexual modes of reproduction. Proliferation by means of bracteate rhizomes is predominant. In this way large clones develop from a single vegetative fragment or seedling.

Inflorescences of *Petasites* are variously described as polygamodioecious, subdioecious, or dioecious. All heads examined by the writer of the taxa concerned here have contained both bisexual disc florets and unisexual pistillate ray florets in varying numbers. Field observations, however, indicate that the plants are functionally dioecious, and are here termed male and female. Heads of the functionally male scapes contain numerous (up to about 60 in var. *palmatus* of Washington) perfect, tubular, disc florets surrounded by a single peripheral row of sterile, pistillate, ray florets. The anthers of the disc florets are the sole source

of viable pollen; their ovaries are sterile. In contrast, heads of functionally female inflorescences contain at their centers only a few (1-5) reduced, perfect but sterile, disc florets. These are surrounded by many (up to about 200 in var. *palmatus* of Washington) fertile, pistillate, ray florets. Seed is formed only in the female inflorescences.

Considering the essentially dioecious nature of the plants and the predominance of vegetative reproduction, it is not unusual to find large colonies or clones which are entirely of one sex or the other. It appears significant, therefore, that extensive searching through the colonies of *Petasites warrenii* over a period of two years has shown that all plants of the taxon are female. This observation also applies to all of the herbarium specimens examined. In addition, innumerable inflorescences were checked at maturity for seed development, but none was found; this suggests the absence of a male pollen parent and of agamospermy.

When both types of inflorescence occur in proximity, pollination, effected by a variety of insects (including butterflies, hoverflies, humble-bees, honey-bees, and beetles on var. *palmatus* in the Puget Sound region), usually takes place and the sexual cycle is completed.

Once the pollen has been shed the male inflorescences quickly wilt and die, while the female inflorescences persist, undergoing considerable increase in height. At maturity the involucre bracts of the fruiting heads reflex, allowing the crowded pappus filaments of the many flowers to expand into a conspicuous, cottony mass. The seeds are carried away on the wind, or fall to the ground.

In the Puget Sound region seeds of var. *palmatus* have been observed to germinate while still attached to the receptacle, while in the laboratory fresh seed will ordinarily germinate on moist filter paper within 24 hours. The period of viability appears to be rather short, however, perhaps as little as a few weeks in duration.

Somatic chromosome counts by Kruckeberg (Ornduff et al. 1943) on plants from the Pacific Northwest indicate that $x = 30$ for *Petasites warrenii*, *P. sagittatus*, and *P. frigidus* var. *palmatus* (*P. speciosus*). Sørensen and Christiansen

(1964), however, report counts of $2n =$ approx. 60 for *P. sagittatus* ($2n = 58, 59, 60$), and *P. frigidus* var. *palmatus* ($2n = 60, 61, 62$), in plants from Fort Chimo, Labrador. The latter authors suggest that the basic chromosome number in the genus *Petasites* is 29, with "A few small chromosomes, presumably B-chromosomes" accounting for the varying numbers in these and other species of the genus.

Herbarium studies

Among herbarium specimens the leaf form of *Petasites warrenii* (Fig. 1D) can be matched by some specimens among the wide variety of forms once relegated to *P. vitifolius* (Fig. 1E, G), but now included with *P. frigidus* var. *nivalis* (Fig. 1H, J). In some instances the varying specimens labeled *P. vitifolius* have been collected in areas where *P. frigidus* var. *palmatus* (Fig. 1A) and *P. sagittatus* (Fig. 1B) are sympatric and growing in close proximity, as is apparent in the collections of Porsild and Breitung along the Canol Road in Yukon Territory, in the collections of McCalla in the vicinity of Banff, Alberta, or in specimens collected by the writer and others on the shores of Lake Itasca, Clearwater Co., Minnesota.

The ranges of the taxa primarily concerned in this pattern of hybridization, as determined from the label data of herbarium specimens and from the writer's observations in the field, are discussed below. Their general distribution in the Pacific Northwest is illustrated in Fig. 4.

Petasites frigidus var. *palmatus* (Ait.) Cronq. (Fig. 1A) spans the North American continent. It ranges from Newfoundland south to New York, and westward through the border provinces of Canada and the northern portions of Michigan, Wisconsin, and Minnesota, to Vancouver Island, British Columbia. In the continental interior it extends northward to southeastern Yukon, and to the arctic coast of the Northwest Territories, where the segregate species *P. arcticus* Porsild (Porsild 1943, p. 74) has been described on the basis of collections of var. *palmatus* from the Mackenzie River delta area. On the west coast a robust ecotype, formerly designated *P. speciosus* (Nutt.) Piper,

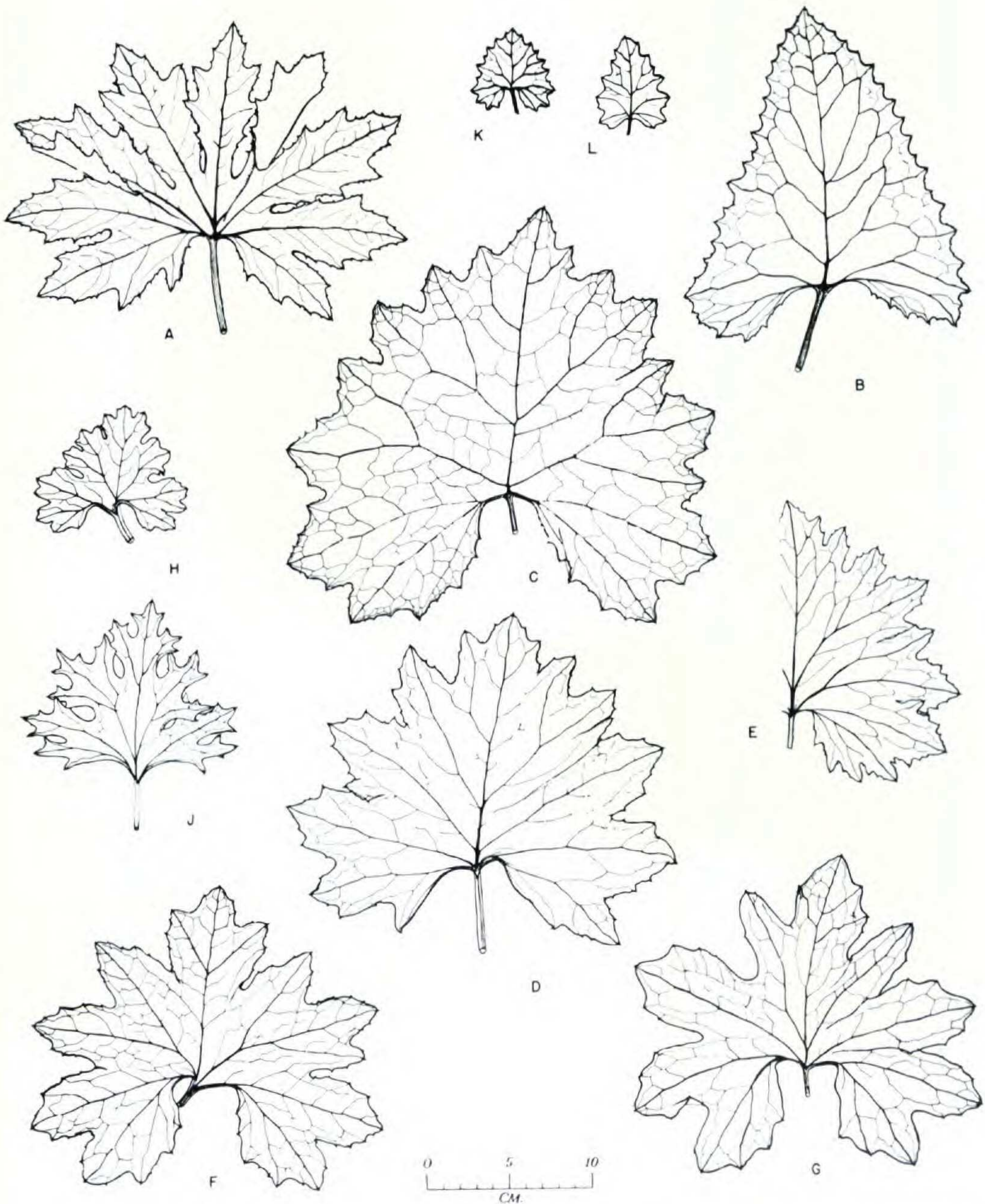


Figure 1. A. *Petasites frigidus* var. *palmatus* (*P. speciosus*), B. *P. sagittatus*, C.-G. various forms of the hybrid *P. × vitifolius*. C. *P. sagittatus* × *frigidus* var. *palmatus*, D. *P. warrenii*, E. *P. vitifolius*, McCalla 9367. Vermillion Lake, Banff, Alberta, (labeled *P. palmatus*), F. *P. warrenii* × *frigidus* var. *palmatus*, G. *P. vitifolius* Itasca State Park, Minnesota, H. *P. frigidus* var. *nivalis* Mt. Rainier National Park, Washington, J. *P. frigidus* var. *nivalis* Mt. Garibaldi, Garibaldi Provincial Park, British Columbia, K. *P. frigidus* var. *frigidus*, Coll: Montell Lappland (Finland), L. *P. frigidus* var. *frigidus*, Spetzman 873. Alaska, Arctic slope.

inhabits the cool, moist, western slopes of the Cascade and Coast ranges to altitudes of about 2500 feet, and ecologically favorable places in the valleys of the foothills on the east side of the Cascades in Washington and Oregon (Fig. 4). The variety also has a far-eastern distribution in Sakhalin (Sugawara 1940), where the segregate species *P. tatewakianus* Kita. has been designated (Kitamura 1940), and the natural hybrid *P. japonicus* subsp. *giganteus* × *P. tatewakianus* Kita. described (Kitamura 1942, p. 165).

Plants of var. *palmatus* thrive in the moist soils or wet clays of disturbed sites such as stream banks, road cuts and embankments, or logging roads in the Pacific Northwest, and in the moist soils of the forest floor in Minnesota.

The range of *Petasites sagittatus* (Pursh) Gray (Fig. 1B) extends from Labrador westward through Canada to British Columbia, Yukon, and on into Alaska (see map no. 322 in Porsild 1957). It occurs in northeastern Washington (Fig. 4), northern Minnesota, and southward sporadically in the Rockies from Idaho and eastern Montana to southern Colorado. A large portion of its range overlaps that of var. *palmatus*, and in some places they may be found growing in close proximity.

Plants of the species observed by the writer in Washington, Colorado, and Minnesota have invariably been growing in shallow standing water or marshy situations, with their rhizomes buried to a depth of several inches in the soft mud.

The first collection of *Petasites warrenii* St. John (Fig. 1D) was made by F. A. Warren in 1926 along Swauk Creek, near the town of Liberty, in the Wenatchee Mountains of Kittitas County, Washington (Fig. 2, 4). Field work in the area has revealed its distribution to be restricted to the moist or wet soils of stream banks, or soft muds of marshy alluvial flats along the courses of three streams: the Boulder, Williams, and Swauk creeks (Fig. 2). Boulder Creek drains into Williams Creek, which flows through the old goldminers' town of Liberty and empties into Swauk Creek. The scattered colonies of *P. warrenii* found along Swauk Creek and lower Williams Creek have probably

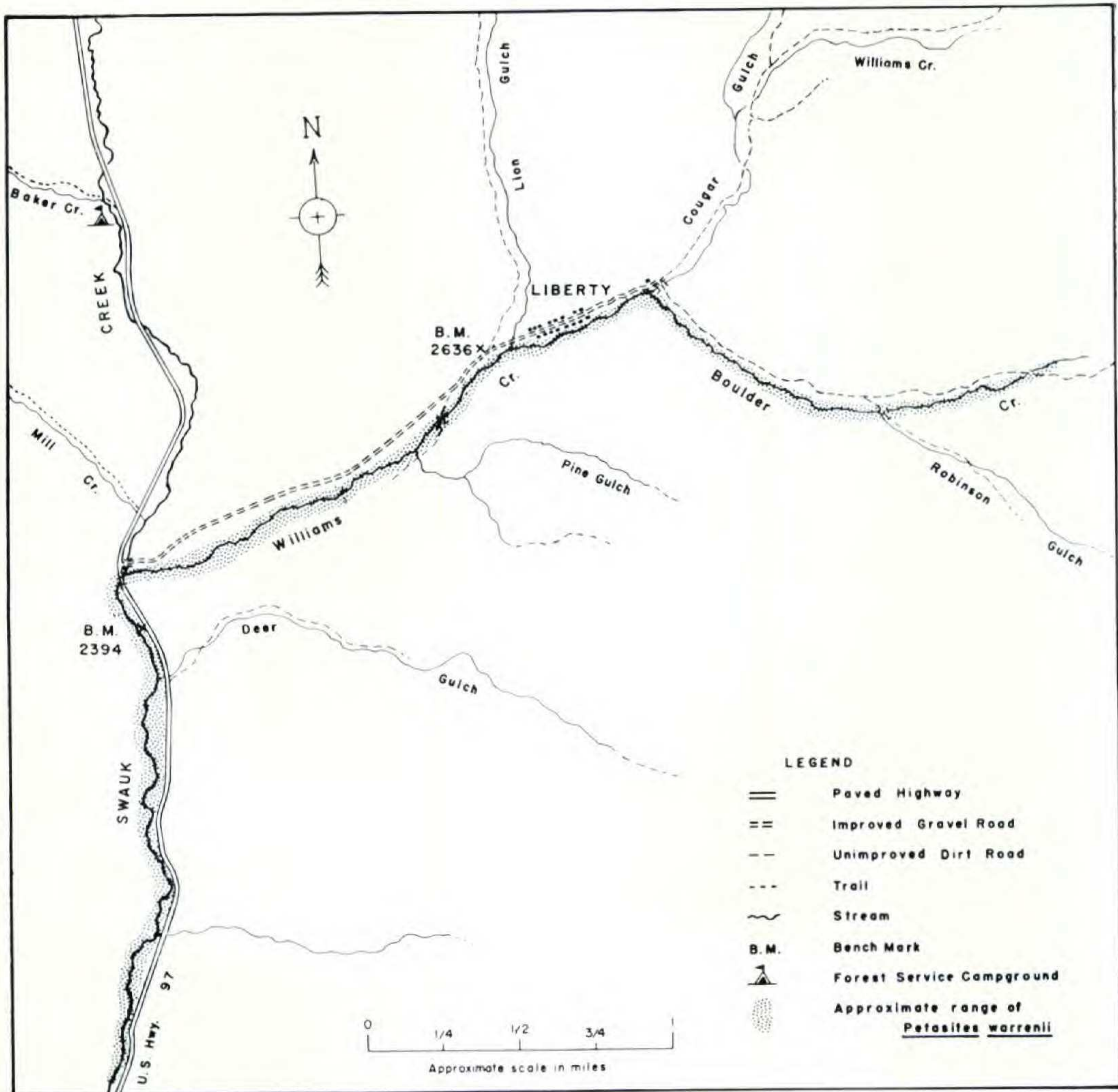


Figure 2. Distribution of *P. warrenii* = *P. × vitifolius* in area of Liberty, Kittitas Co., Washington.

developed clonally from fragments of rhizome washed downstream from the areas of most extensive development along Boulder Creek. The linear distance of distribution along the three streams is roughly six miles.

Occasional plants of *Petasites frigidus* var. *palmatus* are found in ecologically favorable situations along these streams, and one pistillate clone has been observed growing within a large colony of *P. warrenii*. These scattered plants probably arise from seeds carried across the mountains on the wind from the main area of distribution on the west side of the Cascades.

Petasites vitifolius Greene (Fig. 1E, G) is known from lower elevations in British Columbia and Alberta, and eastward to northern Minnesota and the Gaspé Peninsula of Quebec. This distribution covers essentially that portion of the continent in which the ranges of var. *palmatus* and *P. sagittatus* coincide. Plants of the taxon utilize the habitats of either putative parent, but do best in the marshy conditions typical of *P. sagittatus*.

Results of artificial hybridizations.

Seed production in plants artificially pollinated in the field was low. Thirty-seven apparently viable seeds were recovered from inflorescences of *Petasites warrenii*. Results were considerably better in the greenhouse, where 458 apparently good seeds were taken from *P. warrenii* heads, and 111 from heads of *P. sagittatus*. Fruits containing viable seeds can be recognized by their larger size, turgid condition, and light- to dark-brown color. Ovaries in which embryos fail to develop are small, withered, and lack color. In addition, seed development is accompanied by a considerable elongation of the pappus. Visual inspection is sufficient for separation.

Some of the hybrid seed obtained was immediately germinated, and mature plants have since developed and flowered in the greenhouse. These hybrids may be tentatively designated as *Petasites sagittatus* × *frigidus* var. *palmatus*, and *P. warrenii* × *frigidus* var. *palmatus*. They are discussed briefly below, and the forms of their leaves and style branches are compared with those of the parents in figures 1 and 3 respectively.

Petasites sagittatus × *frigidus* var. *palmatus*. (Fig. 1C).

Mature leaves of this F₁ hybrid are shallowly lobed, with the lobes entire to sinuate-dentate, or again shallowly lobed. In Fig. 1 the general leaf form of this hybrid (Fig. 1C) is compared with those of the other North American taxa, including: *Petasites warrenii* (Fig. 1D); a leaf representative of collections, variously labeled *P. vitifolius* or *P. palm-*

atus, made by McCalla in the vicinity of Banff, Alberta (Fig. 1E); two specimens of *P. frigidus* var. *frigidus* (Fig. 1K, L), to which *P. warrenii* is attributed; and two leaves of *P. frigidus* var. *nivalis* (Fig. 1H, J), to which the various forms of *P. vitifolius* are attributed.

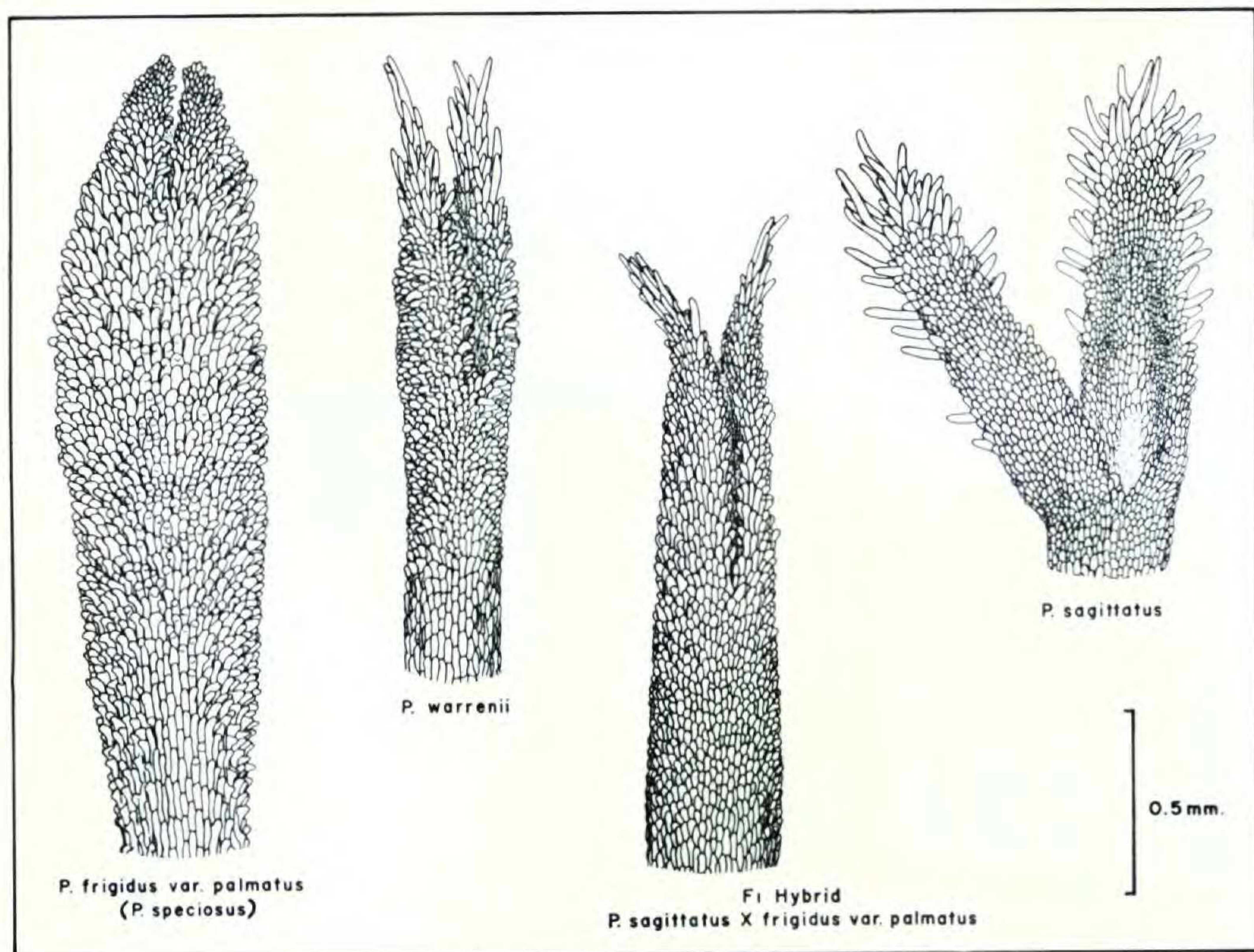


Figure 3. Comparison of the style branches of parent and hybrid forms.

The style branches of the parental taxa, the artificial F_1 hybrid, and *Petasites warrenii* are compared in Fig. 3. The styles of *P. frigidus* var. *palmatus* (*P. speciosus*) are clavate, with a very shallow notch about 0.5 mm deep at the tip. The surface of the entire style tip is papillose, with no elongated setae. The styles of *P. sagittatus* bear more or less oblong branches which are about 1.0-1.5 mm long, with long sweeping hairs clothing the margins and tips. In *P. warrenii*, and *P. sagittatus* \times *frigidus* var. *palmatus*, the style branches are more or less intermediate in length, and terminate in elongate hairs very similar to those in *P. sagittatus*, but their margins are merely papillose. The style

branches of both the artificial and supposed natural hybrids thus compare favorably in form, and are intermediate between those of the parental taxa. Although the styles illustrated here were taken from the somewhat reduced, sterile, disc florets of the female heads of the four taxa, comparison with their larger, fertile counterparts in the male heads (with the exception of *P. warrenii*) shows their form to be representative.

The form of the bracts of the inflorescence scape, the margins of the involucrel phyllaries, and of the flags of the anther connectives (although not illustrated here) also compare favorably among the artificial and supposed natural hybrids, and are intermediate between those of the parent taxa (cf. illustrations in Bogle 1961).

Petasites warrenii × *frigidus* var. *palmatus*. (Fig. 1F).

If, on the basis of the foregoing morphological evidence, a hybrid origin similar to the above can be accepted for *Petasites warrenii*, then the combination *P. warrenii* × *frigidus* var. *palmatus* is the equivalent of a backcross of an F₁ hybrid to the palmate parent. Leaf form among progeny of *P. warrenii* × *frigidus* var. *palmatus* does not exhibit the relative uniformity seen in offspring of *P. sagittatus* × *frigidus* var. *palmatus*, and the lobing is deeper than that of the F₁ hybrids. It was found that the various forms recovered among the backcross progeny compare favorably with many of the variations of *P. vitifolius* found in nature. The mature leaf form of one of these hybrids (Fig. 1F) is compared with that of a collection of *P. vitifolius* from Itasca State Park, Minnesota (Fig. 1G), and with leaves of *P. frigidus* var. *nivalis* of alpine habitats in the Cascade mountains of Washington and British Columbia (Figs. 1H, J), the variety to which *P. vitifolius* has been subordinated.

Pollen viability

Pollen grains from available male plants were stained in lactophenol-aniline blue to obtain a rough measure of pollen viability. Two to four flowers from each inflorescence were

tested, and a minimum of 200 grains were counted for each flower. The number of plants tested is indicated in parentheses after each binomial. The ranges of stainability percentages found are as follows:

<i>P. frigidus</i> var. <i>palmatus</i> (<i>P. speciosus</i>), (3)	95-99%
<i>P. sagittatus</i> × <i>frigidus</i> var. <i>palmatus</i> , (10)	29-99
<i>P. warrenii</i> × <i>frigidus</i> var. <i>palmatus</i> , (3)	29-44
<i>P. vitifolius</i> , (1)	45-63

Although the range of stainability is rather wide in *Petasites sagittatus* × *frigidus* var. *palmatus*, more than half of the counts obtained are in excess of sixty percent. Viability may vary considerably from flower to flower within an inflorescence, but in most cases the extremes of range are from different plants rather than from flowers of the same plant. Increased complexity of the genome, as in *P. warrenii* × *frigidus* var. *palmatus*, appears to be accompanied not only by reduced pollen viability, but by increased variability in the size of pollen grains and in the stainability of their protoplasts; it thus becomes increasingly difficult to distinguish between viable and inviable grains.

DISCUSSION

The opinions of Hooker, Herder, and Cronquist reflect the impression given by herbarium specimens that the three morphological "peaks" of leaf form embodied in the varieties of *Petasites frigidus* (Fig. 1) are almost completely intergrading. Hooker (1833) maintained *P. sagittatus* as a species, while suggesting that it, too, intergrades with the other forms. Cronquist considers *P. sagittatus* sufficiently distinct to be maintained as a separate species. The evidence presented above, however, suggests that *P. warrenii*, and many of the variants formerly lumped in *P. vitifolius* but now assigned to *P. frigidus* var. *nivalis*, are actually manifestations of hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus*.

Many of the various leaf forms of putative hybrid origin found in nature can be matched by similar forms found among the artificially created hybrid progeny. The morphological intermediacy seen in the leaves and style

branches of *Petasites warrenii* and the artificial F_1 hybrids is also apparent in their inflorescence bracts, phyllaries, and anther connectives. Such intergradation of form could doubtless be demonstrated in other areas of the continent where hybrids are being formed, but the F_1 hybrids should be expected to reflect the morphological variation seen in the parent taxa from different geographical areas. The deeper, narrower lobing of midwestern representatives of var. *palmatus*, for example, may result in deeper lobing in F_1 hybrids than that apparent in *P. warrenii* and the artificial F_1 hybrid illustrated here, both of which reflect the broader, more shallowly lobed west coast phase of var. *palmatus* (i.e., *P. speciosus*).

Pollen stainability percentages indicate high fertility, or at least some fertility, in plants of both the F_1 and more complex hybrid generations. Such fertility in nature has probably enhanced the variation among hybrids through

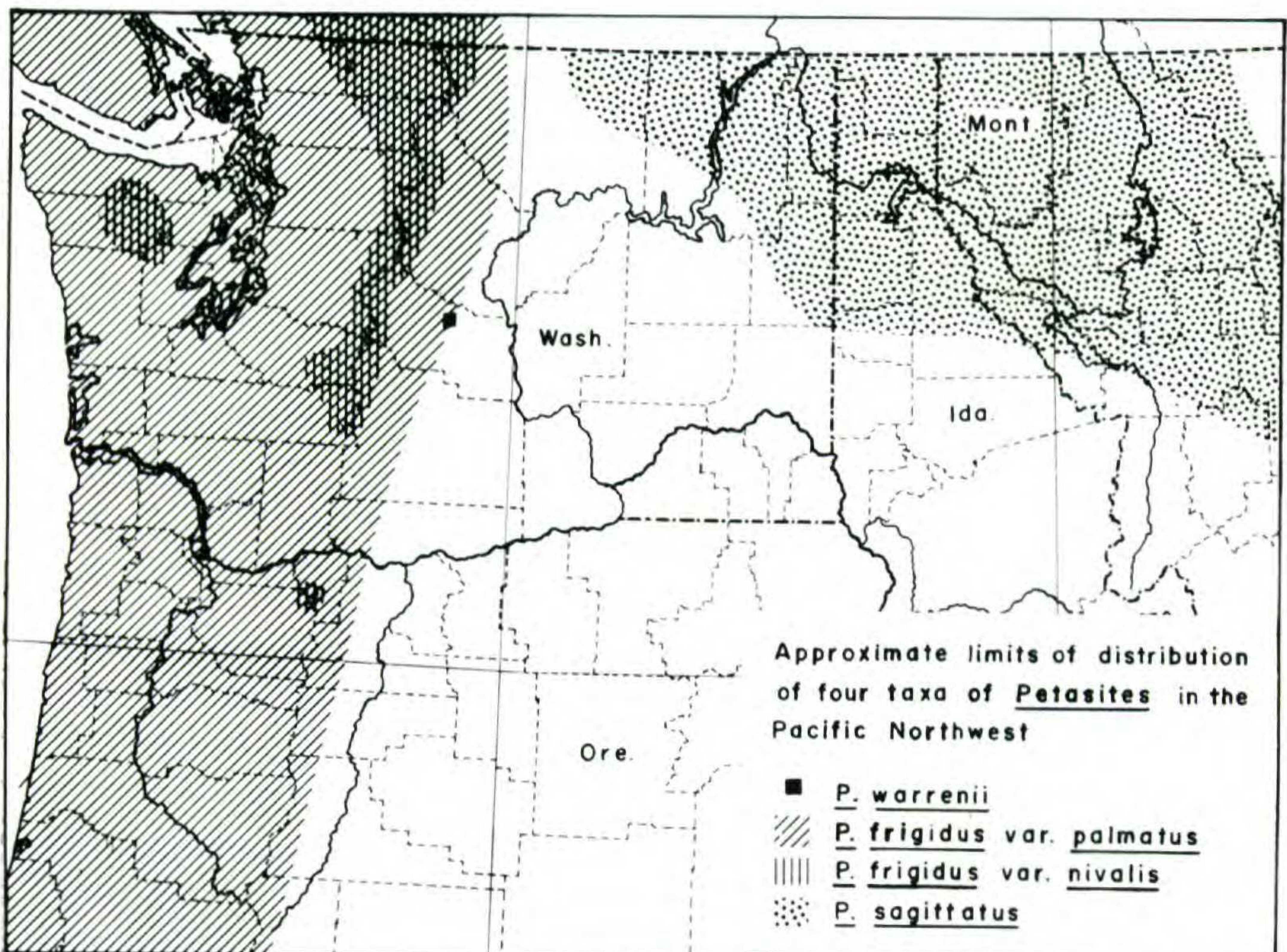


Figure 4. Approximate limits of distribution of four taxa of *Petasites* in the Pacific Northwest.

the formation of F_2 and F_3 combinations, and backcrossing of these to the parent stocks.

It is now necessary to remove the taxa of hybrid origin from synonymy under the varieties of *Petasites frigidus*, and to consider the position of *P. sagittatus*. Removal of *P. warrenii* from var. *frigidus* eliminates the variety from the State of Washington, restricting the southern limit of its range to northern British Columbia. Transfer of *P. vitifolius* from var. *nivalis*, however, shrinks the transcontinental range of the variety to a much smaller arctic-alpine distribution in northwestern North America, where it then consists only of the former species *P. nivalis* Greene (Fig. 4) and *P. hyperboreus* Rydb. Even with *P. vitifolius* removed var. *nivalis* remains a polymorphic group of unknown origin, possibly arising in hybridization between *P. frigidus* var. *frigidus* and var. *palmatus*, as suggested by Hultén (1950, p. 1583).

With regard to the position of *Petasites sagittatus* it could be argued that there is now a basis for reducing the species to varietal status within the *P. frigidus* complex if genetic compatibility and interspecific hybridization are to be the criteria for classification. Hultén (1950, p. 1583), however, does not agree with the idea of uniting such diverse forms under a single specific epithet. He would prefer to maintain the varieties as distinct species and recognize the hybrids under formula designations. The latter is the course preferred by the writer in the case of *P. sagittatus*. The link of hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus* is strong. On the basis of four collections from widely scattered points in Alaska and Yukon, Hultén has also proposed hybridization between *P. sagittatus* and *P. frigidus* var. *frigidus* (see map 1177c, Hultén 1950). But in neither case of hybridization is the characteristic form of *P. sagittatus* "swamped" by the hybrid intermediates.

On the basis of herbarium studies the areas of primary hybridization to the south, at least, appear to be few. The number of probable F_1 specimens similar to those illustrated here is also few compared with the number representing

apparently more complex hybrid combinations such as *Petasites warrenii* \times *frigidus* var. *palmatus*. Wide dispersal of wind borne hybrid seed may magnify the extent of actual primary hybridization between the parent species, while persistence of hybrid plants through vegetative reproduction may greatly increase the period of time, as well as the number of individuals, available for further hybridization. *P. warrenii* is a case in point. Its exact origins are unknown. It may have developed from a chance hybrid seed blown in from some area to the north where the putative parents are hybridizing, or it may have arisen through hybridization in the Swauk valley if *P. sagittatus* occurred there in the past. Occasional female plants of var. *palmatus* have been found among the colonies of *P. warrenii*. Should a male plant of var. *palmatus* become established among the strictly female clones of *P. warrenii* a new phase of hybridization could begin.

In the southern portions of their ranges *Petasites sagittatus* and *P. frigidus* var. *palmatus* are distinct morphologically and ecologically, and their hybrid offspring are recognizable. The writer feels that extensive field work and detailed study in critical northern areas, to delimit more precisely the varieties and their inter-relationships, should precede expansion of the *P. frigidus* complex to include *P. sagittatus*.

CONCLUSIONS

Petasites warrenii and *P. vitifolius* (including *P. trigonophyllus*) are merely phases of a large and very variable group originating in hybridization between *P. sagittatus* and *P. frigidus* var. *palmatus*. Repeated interbreeding among hybrids, and backcrossing to the parent stocks, has probably occurred, producing the wide range of variability now seen among the hybrids. The following hybrid designation is proposed to include the intermediate forms:

Petasites \times *vitifolius* Greene (pro sp.) = *P. sagittatus*
 \times *P. frigidus* var. *palmatus*.

P. warrenii St. John, Res. Stud. State Coll. Wash.
1:109. 1929.

P. vitifolia Greene, Leaflet 1:180. 1906.

P. trigonophylla Greene, Leaflet 1:180. 1906.

Listed below are the herbarium specimens examined during this investigation which are considered to be of hybrid origin. The specimens of all taxa examined and annotated are listed in a previous paper (Bogle 1961). Abbreviations used to designate herbaria are those proposed by Lanjouw and Stafleu (1959). Specimens of the artificial hybrids synthesized during this study are on deposit in the herbaria of the University of Washington, the University of Minnesota, and the Gray Herbarium of Harvard University.

Abbe, Abbe, & Marr 3221 (MIN, US); Ahlgren 1032 (MIN); Anderson, J. P. 10414 (ISC); Anderson, J. R. (WSU 44648); Becket M-55-23 (MIN); Breitung 1794, 15862 (UAC); Brinkman 4254 (US); Brown 45 (ISC); Butters, Huff, & Rosendahl 2755 (MIN); Campbell 150, 569 (CAN); Eastham (UBC 11922a, 11922b); Eastwood 476 (CAN, WS), 481 (US, WS); Fernald & Collins 259 (MIN, US); Fernald, Griscom, & Mackenzie 26080 (US); Garton 1455 (US), 2641, 8530 (MIN); Gillet 2315 (US); Harper 3078 (MIN); Hitchcock & Marsh 3283 (WTU, WS); Krivda 1861 (UBC); Lakela 1137a (MIN, US), 8081, 8252, 11633, 12882, 18258, 20587 (MIN); Lewis 306 (US); Macoun 6/10/1880 [TYPE of *P. vitifolius*] (US), (WSU 46231); Marie-Victorin & Rolland-Germain 27567 (US); Marie-Victorin, Rolland-Germain, & Louis-Marie 21232 (US); McCalla 2059a, 3704, 7061, 11310 (UAC), 9192, 9235, 9275, 9284, 9367, 9560, 9580 (UBC); Moir 812, 947, 1107, 1435, 2010, 2040 (MIN); Moore & Moore 11028 (MIN); Moss 2006, 2355, 4219, 4264, 8846 (UAC); Moyle 948, 1091 (MIN); Nelson 2426 (MIN); Ownbey 3216 (MIN); Porsild & Breitung 9342, 9424 (CAN), 9759 (WTU), 10333 (CAN, ISC), 10334 (ISC), 11733 (US); Richards 4763 (MIN); Richardson 14678 (CAN); Rosendahl 4752 (MIN); Rosendahl & Moyle 2218 (MIN); Sandberg 155a [TYPE of *P. trigonophyllus*] (US, WS), (US 45059), (MIN 212577); Scoggan 5141, 5667 (UAC); St. John, English, Jones, & Mullen 8106 (WS); Taylor & Lewis 392 (UBC); Thompson 5961, 8204 (WTU), 11310 (MONTU, WS, WTU), 14503 (ID, MIN, UAC, UBC, WS); Tisdale (UBC 8736); Turner 1725, 4367, 4514 (UBC), 4364, 4367, 4406, 4413 (UAC); Warren 380, 542 [TYPE of *P. warrenii*], 809 (WS).

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